MycoKeys 109: 31–48 (2024)
DOI: 10.3897/mycokeys.109.129791

Research Article

# Morphological and molecular identification of two new *Marasmiellus* species (Omphalotaceae, Agaricales) from Thailand

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This article is part of:
***Exploring the Hidden Fungal Diversity: Biodiversity, Taxonomy, and Phylogeny of Saprobic Fungi***
*Edited by Samantha C. Karunarathna, Danushka Sandaruwan Tennakoon, Ajay Kumar Gautam*

OPEN ACCESS

Academic editor:
Danushka Sandaruwan Tennakoon
**Received:** 16 June 2024
**Accepted:** 29 August 2024
**Published:** 24 September 2024

**Citation:** Lu W, Nutaratat P, Kumla J, Tibpromma S, Elgorban AM, Karunarathna SC, Suwannarach N (2024) Morphological and molecular identification of two new *Marasmiellus* species (Omphalotaceae, Agaricales) from Thailand. MycoKeys 109: 31–48. https://doi.org/10.3897/mycokeys.109.129791

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## Abstract

*Marasmiellus* (Omphalotaceae, Agaricales) specimens collected in Thailand were investigated based on morphological characteristics and molecular phylogenetic analyses. In the present study, two species are introduced as new to science, namely *Marasmiellus thailandicus* and *M. minutisporus*. Phylogenetic analyses were carried out based on the internal transcribed spacer (nrITS) and nuclear ribosomal RNA large subunit (nrLSU) regions, and the results revealed that the two new taxa are distinct species within *Marasmiellus*. Another specimen was identified as *M. scandens* and is reported for the first time with morphology and molecular data from Thailand. Descriptions, illustrations, and phylogenetic results are provided. In addition, *M. diaphanus* and *M. colocasiae* are proposed as new combinations of *Collybiopsis diaphana* and *Paramarasmius colocasiae*, respectively, based on the phylogenetic evidence.

**Key words:** Basidiomycota, new taxa, omphalioid mushroom, taxonomy, wood-decaying mushroom

## Introduction

The genus *Marasmiellus* Murrill was proposed by Murrill (1915), with the type species *M. juniperinus* Murrill [treated as *Collybiopsis juniperina* (Murrill) R.H. Petersen] (Petersen and Hughes 2021). This is one of the well-known and widely distributed genera, which belongs to the family Omphalotaceae Bresinsky, order Agaricales Underw. with a worldwide distribution in the tropics and the subtropics (Moncalvo et al. 2002; Wilson and Desjardin 2005; Blanco-Dios 2015; Sesli et al. 2018). Most species of this genus are saprobes

occurring on decaying plant matter, which degrade leaf and woody debris, some species are host-specific, parasitic, and attack various economically important plants (e.g., banana, coconut, and sugar cane) (Singer 1973; Jabeen et al. 2023). *Marasmiellus* species are characterized by collybioid, omphalioid, or pleurotoid basidiomata, slightly decurrent, pileus white, yellow, pink or brown, convex, lamellae well-developed, intervenose, adnate to decurrent, and smooth, white or hyaline, thin-walled, and ellipsoid to oblong, rarely subcylindrical, fusiform, inamyloid basidiospores, usually with confluent hilar appendage, and pileipellis or stipitipellis with a Rameales-structure (Singer 1973; Pérez-De-Gregorio et al. 2011). Prior to this study, eight *Marasmiellus* species, including *M. albofuscus* (Berk. & M.A. Curtis) Singer (Chandrasrikul et al. 2011), *M. alliiodorus* (Mont.) Singer (Chandrasrikul et al. 2011), *M. amygdalosporus* Pegler (Chandrasrikul et al. 2011), *M. candidus* (Fr.) Singer (Seephueak et al. 2018), *M. chamaecyparidis* (Hongo) Hongo (Chandrasrikul et al. 2011), *M. collybioides* (Speg.) J.S. Oliveira, *M. corticum* Singer (Seephueak et al. 2018), and *M. paspali* (Petch) Singer (Chandrasrikul et al. 2011) have been reported from Thailand.

Some phylogenetic studies on Omphalotaceae based on nrITS and nrLSU in single and multigene analyses have been conducted to solve the stable placement where *Gymnopus* (Pers.) Gray and *Marasmiellus* still remain uncertain. Initially, *Gymnopus* and *Marasmiellus* were treated as multiple branches, nonmonophyletic groups (Moncalvo et al. 2002; Mata et al. 2004; Wilson and Desjardin 2005; Hughes et al. 2010; Petersen and Hughes 2017). Mata et al. (2004) argued for proposing the broad concept of *Gymnopus* based on nrITS analysis which places the type species of *Marasmiellus* within a *Gymnopus* clade. However, Wilson and Desjardin (2005) argued for keeping *Marasmiellus* and *Gymnopus* as distinct genera. In addition, Oliveira et al. (2019) provided consistent evidence for more restricted *Gymnopus* and a distinct *Marasmiellus* s. str., which is composed of *Gymnopus* sect. *Vestipedes* and members of *Marasmiellus* sect. *Dealbati*, *Marasmiellus*, *Rameales*, and *Stenophylloides*.

According to the recent nomenclature, the type species of *Marasmiellus* (*M. juniperinus* Murrill) was transferred to *Collybiopsis* (J. Schröt.) Earle. Petersen and Hughes (2021) considered *Marasmiellus* as a synonym of *Collybiopsis*, while the concepts of *Collybiopsis* between Oliveira et al. (2019) and Petersen and Hughes (2017) are different. In addition, the boundaries among *Gymnopus*, *Marasmiellus*, and *Collybiopsis* would be more blurred, especially between *Marasmiellus* and *Collybiopsis*, as well as if these species were transferred to *Collybiopsis*, then it would be polyphyletic with *Rhodocollybia* Singer, *Paragymnopus* J.S. Oliveira, and *Lentinula* Earle would be a synonym of *Gymnopus*. Nevertheless, further clarifications are needed for whether *Collybiopsis* accommodates all members of *Marasmiellus*. In this study, we treat *Marasmiellus* following Singer's (1974, 1986) concept.

The present study aims to describe two new *Marasmiellus* species and a new report of *M. scandens* (Massee) Dennis & D.A. Reid collected from Thailand based on morphological characteristics and multigene phylogenetic analyses. In addition, we propose two new combinations of *Collybiopsis diaphana* and *Paramarasmius colocasiae*. Descriptions, illustrations, and a phylogenetic tree to show the placement of the taxa are provided.

## Materials and methods

### Morphological study

Fresh basidiomata were collected from the northern part (Chiang Mai University, Chiang Mai Province) and the southern part (Phatthalung Province) of Thailand. Macromorphological features of the basidiomata were documented and photographed in the field. Color names and codes were determined following Kornerup and Wanscher (1978). The specimens were taken back to the laboratory, dried completely in an electric oven at 45 °C (Hu et al. 2022), and sealed in plastic bags for further micro-morphological characterization. The holotype and other examined specimens were deposited at the Chiang Mai University Biology Department Herbarium (CMUB), Chiang Mai University, Thailand. Freehand sections of the dried specimens were mounted in 5% KOH and Congo red to observe microscopic characteristics, while Melzer's reagent was used to increase the contrast of structures and the amyloid reaction of basidiospores. The light Eclipse 80i microscope (Olympus, Japan) was used to view features of basidia, basidiospores, cystidia, and hyphae, which were drawn by using the drawing tube attached to the microscope. The sizes of micro-structures were calculated based on at least 50 measurements, and the notations (a–) b–c (–d) describe the basidiospore dimensions, where the range 'b–c' represented 90% or more of the measured valued and a and b are the extreme values. The Q refers to the length/width ratio values of all measured basidiospores. Qm refers to the average Q value with standard deviation. 'L' refers to the number of complete lamellae, and 'l' refers to the number of lamellulae between every two complete lamellae. All the line drawings of the microstructures were made freehand based on the rehydrated materials and finally modified using Adobe Illustrator 2019.

### DNA extraction, PCR amplification, and sequencing

The genomic DNA was extracted from fresh specimens using the DNA Extraction Mini Kit (FAVORGEN, China) according to the manufacturer's instructions. Primer pairs ITS1/ITS4 (nrITS) and LR0R/LR5 (nrLSU) regions were amplified by the polymerase chain reaction (PCR) (Vilgalys and Hester 1990; White et al. 1990), which was performed in a total volume of 20 µL reaction containing 1.0 µL DNA template, 1.0 µL each primer, 10.0 µL 2X Quick Taq® HS DyeMix (TOYOBO, Japan) and 7 µL deionized water. The amplification program was performed with an initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30s, annealing at 54 °C for 40 s, and an extension at 72 °C for 1 min, with a final extension at 72 °C for 10 min on a peqSTAR thermal cycler (PEQLAB Ltd., UK). PCR products were checked on 1% agarose gels stained with ethidium bromide under UV light. PCR products were purified using a PCR clean-up Gel Extraction NucleoSpin® Gel and PCR Clean-up Kit (Macherey-Nagel, Germany) following the manufacturer's protocol. The purified PCR products were directly sequenced, and the sequences were automatically determined in the genetic analyzer at 1$^{ST}$ Base Company (Kembangan, Malaysia) with the PCR primers mentioned above. Names of the new taxa were introduced and deposited in MycoBank (https://www.mycobank.org/, assessed on June 12, 2024). All newly generated sequences in the present study were deposited to GenBank (https://www.ncbi.nlm.nih.gov/genbank/, assessed on June 10, 2024).

### Phylogenetic analyses

The newly generated forward and reverse of sequences from this study were assembled in the BioEdit v. 7.0.5 (Hall 1999), then were subjected to BLASTn searches in the GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi, assessed on 10 June 2024) to check those most related with a high degree of similarity taxa (with ≥ 85% query coverage and ≥ 90–100% percent identity), *Moniliophthora perniciosa* (Stahel) Aime & Phillips-Mora (CMR UB 2041) was chosen as the outgroup from the family Marasmiaceae, and were aligned by running MAFFT v.7 at the online website server platform (www.ebi.ac.uk/Tools/mafft, assessed on June 10, 2024) (Katoh and Standley 2013) with additional sequences downloaded from GenBank and previous studies (César et al. 2020; Petersen and Hughes 2020) as is shown in Table 1. Gaps and ambiguous regions were automatically removed by trimAL v1.2 (http://trimal.cgenomics.org, assessed on June 10, 2024), and sequences were manually improved in BioEdit whenever necessary. Both sequencing datasets were combined using SequenceMatrix 1.7.8 (Vaidya et al. 2011) and AliView (Larsson 2014). The final FASTA format was converted to PHYLIP and NEXUS format in the Alignment Transformation Environment (ALTER) online program (Glez-Peña et al. 2010). The phylogenetic analyses were carried out by employing Maximum likelihood analysis (ML) and Bayesian analysis (BYPP) methods. The ML was performed on RAxML-HPC BlackBox (v.8.2.4) (Stamatakis 2014) with 1000 rapid bootstrap replicates on the CIPRES Science Gateway v.3.3 (http://www.phylo.org/portal2, assessed on 10 June 2024; Miller et al. 2010), with the GTRGAMMA substitution model. Bayesian analyses of six simultaneous Markov chains were run for 2,000,000 generations, and trees were sampled and printed to output at every 100$^{th}$ generation (resulting in 20,000 total trees) with the GTR+I+G evolution model that was estimated using MrModeltes v. 2.2 (Nylander 2004). Phylogenetic trees were visualized using FigTree v1.4.0 (Rambaut 2009). The reliable bootstrap support values of ML (BS ≥ 60%) and BI (PP ≥ 0.90) were inserted above the nodes.

## Results

### Phylogenetic analyses

In the dataset, the combined nrITS and nrLSU sequence dataset consisted of a total number of 86 taxa, and the aligned dataset was comprised of 1593 characters, including gaps (nrITS: 1–709 and nrLSU: 710–1593). The best RAxML tree was obtained with a final ML optimization likelihood value of -15536.515830. The matrix had 780 distinct alignment patterns, with 34.45% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.248165, C = 0.187111, G = 0.251637, T = 0.313087, with substitution rates AC = 1.027131, AG = 5.242142, AT = 1.916708, CG = 0.743477, CT = 6.311829, GT = 1.000000; gamma distribution shape parameter $\alpha$ = 0.681313, tree-Length = 3.382466. Notably, the phylograms of the ML and BI analyses were similar in topology. Therefore, the phylogenetic tree obtained from ML analysis was selected and is presented in this study (Fig. 1).

**Table 1.** Names, voucher numbers, countries, and corresponding GenBank accession numbers of the taxa used in the phylogenetic analyses of this study.

| Taxa Name | Voucher | Country | GenBank Accession Number | |
|---|---|---|---|---|
| | | | nrITS | nrLSU |
| *Collybiopsis biformis* | TENN58541 | USA | DQ450054 | NA |
| *C. biformis* | HMJAU61116 | China | OQ597035 | OQ594445 |
| *C. brunneogracilis* | SFSU-AWW01 | Indonesia | AY263434 | NA |
| *C. carneopallida* | BRNM:747442 | Italy | OM522632 | NA |
| *C. clavicystidiata* | SFC20180705–84 | South Korea | OL467252 | OL462817 |
| *C. confluens* | HMJAU61120 | China | OQ597037 | NA |
| *C. confluens* | TENN50524 | Sweden | DQ450044 | NA |
| *C. confluens* | TENN-F-067864 | Germany | KP710296 | NA |
| *C. diaphana* | Cesar202 | Mexico | MT232390 | NA |
| *C. diaphana* | Cesar44 | Mexico | MT232391 | NA |
| *C. furtive* | SFSU-F-024524h1 | USA | MN413341 | NA |
| *C. furtive* | SFSU-F-024524h2 | USA | MN413342 | NA |
| *C. istanbulensis* | KATO fungi 3596 | Turkey | KX184795 | KX184796 |
| *C. juniperina* | TENN59540 | USA | AY256708 | KY019637 |
| *C. juniperina* | TENN-F-58988 | Argentina | KY026661 | KY026661 |
| *C. luxurians* | TENN-F-057910 | USA | AY256709 | AY256709 |
| *C. luxurians* | HMJAU61101 | China | OQ597045 | OQ594455 |
| *C. luxurians* | HMJAU61198 | China | OQ597046 | OQ594456 |
| *C. melanopus* | SFSU AW54 | Indonesia | OR818034 | OR817634 |
| *C. melanopus* | CUH AM093 | India | KM896875 | KP100305 |
| *C. orientisubnuda* | NIBRFG0000500990 | Turkey | OL467262 | OL546546 |
| *C. peronata* | TENN-F-065120 | Belgium | KY026677 | KY026677 |
| *C. quercophila* | TENN-F-69267 | Slovakia | KY026729 | NA |
| *C. quercophila* | TENN-F-69320 | USA | KY026736 | NA |
| *C. ramealis* | TENN-F-065146 | Belgium | MN413346 | MW396882 |
| *C. ramealis* | TENN-F-065145 | Belgium | MN413345 | MN413345 |
| *C. ramulicola* | GDGM44256 | China | KU321529 | NA |
| *C. stenophylla* | TENN-F-051099 | USA | MN413330 | MW396887 |
| *C. stenophylla* | TENN-F-065943 | USA | MN413331 | MW396886 |
| *C. ugandensis* | SFSU-BAP 614 | Sao Tome | MF100986 | NA |
| *C. vellerea* | SFC20140821-29 | South Korea | OL467267 | OL462810 |
| *Gymnopus alkalivirens* | TENN51249 | USA | DQ450000 | NA |
| *G. brunneiniger* | XAL-Cesar 49 | Mexico | MT232389 | NG075396 |
| *G. efibulatus* | HGASMF01-7052 | China | OM970865 | OM970865 |
| *G. fusipes* | TENN59300 | China | AF505777 | NA |
| *G. fusipes* | TENN59217 | France | AY256710 | AY256710 |
| *Marasmiellus agrianum* | NJ201111 | Pakistan | MZ044839 | NA |
| *M. agrianum* | NJ201112 | Pakistan | MZ044840 | NA |
| *M. alnicola* | URM90019 | Brazil | KY302681 | KY302682 |
| *M. bicoloripes* | CAL1524 | India | KY807129 | KY817233 |
| *M. candidus* | CBS:252.39 | USA | MH856003 | NA |
| *M. candidus* | MSM#0017 | Pakistan | KJ906507 | NA |
| *M. celebanticus* | TO HG2281 | Spain | JF460781 | NA |

| Taxa Name | Voucher | Country | GenBank Accession Number | |
|---|---|---|---|---|
| | | | nrITS | nrLSU |
| *M. gregarius* | G0197 | Japan | NA | MK278330 |
| *M. griseobrunneus* | AMH 10117 | India | MK656132 | MK660195 |
| *M. griseobrunneus* | CAL 1752 | India | MK660191 | MK660192 |
| *M. griseobrunneus* | AMH 10118 | India | MK660194 | MK660193 |
| *M. lucidus* | s1 | China | OP459424 | NA |
| *M. lucidus* | HT10 | Japan | AB968237 | AB968237 |
| ***M. minutisporus*** | **CMUB40054** | **Thailand** | **PP889931** | **PP890011** |
| ***M. minutisporus*** | **CMUB40055** | **Thailand** | **PP889932** | **PP890012** |
| *M. omphaloides* | PDD:95810 | New Zealand | HQ533031 | NA |
| *M. paspali* | AHH65 | USA | EF175515 | NA |
| *M. paspali* | AHH26 | USA | EF175511 | NA |
| *M. pilosus* | iNat91483993 | Cayman Islands | OP651730 | NA |
| *M. rhizomorphogenus* | BRNM:715003 | South Korea | GU319116 | GU319120 |
| *M. scandens* | GH-80 | Ghana | MN794179 | NA |
| *M. scandens* | GH-21 | Ghana | MN794139 | NA |
| *M. scandens* | KUNCC22-12451 | China | OP536418 | NA |
| ***M. scandens*** | **CMUB40056** | **Thailand** | **PP889933** | **PP890013** |
| ***M. thailandicus*** | **CMUB40052** | **Thailand** | **PP889929** | **PP890009** |
| ***M. thailandicus*** | **CMUB40053** | **Thailand** | **PP889930** | **PP890010** |
| *M. tenerrimus* | TENN61596H1 | USA | FJ596840 | NA |
| *M. tenerrimus* | TENN61596H2 | USA | FJ596841 | NA |
| *M. tricolor* | M01452 | Estonia | LR872638 | NA |
| *M. venosus* | TNS-F-52281 | Japan | AB968236 | NA |
| *M. violaceogriseus* | PDD:95788 | New Zealand | HQ533014 | NA |
| *M. volvatus* | URM 84466 | Brazil | KC348449 | KC348442 |
| *M. sacchari* | CBS:215.32 | USA | NA | MH866745 |
| *Moniliophthora perniciosa* | CMR UB 2041 | Brazil | AY317136 | NA |
| *Paragymnopus foliiphilus* | TENN-F-68183 | USA | KY026705 | KY026705 |
| *P. perforans* | TENN-F-50318 | Sweden | KY026623 | KY026623 |
| *P. perforans* | TENN-F-50319 | Sweden | KY026624 | KY026624 |
| *P. pinophilus* | TENN-F-69207 | USA | KY026725 | KY026725 |
| *Paramarasmius colocasiae* | SP376044 | Brazil | GQ452780 | NA |
| *Pa. mesosporus* | TNS-T-48339 | Japan | OM522625 | OM522623 |
| *Pa. palmivorus* | AKD 112/2015 | India | MG251431 | MG251441 |
| *Paramycetinis austrobrevipes* | TENN-F-50135 | Australia | KY026622 | KY026622 |
| *Par. caulocystidiatus* | TENN-F-5405 | New Zealand | KY026645 | NA |
| *Pseudomarasmius efibulatus* | TENN-F-56187 | New Zealand | MK268234 | NA |
| *Ps. glabrocystidiatus* | BRNM 718676 | Korea | NR152899 | KF251093 |
| *Ps. nidus-avis* | Cesar36 | Mexico | MH560576 | NA |
| *Ps. pallidocephalus* | TENN-F-52401 | USA | KY026635 | KY026635 |
| *Ps. patagonianus* | TENN-F-54424 | Chile | KY352649 | NA |
| *Ps. quercophylloides* | TENN-F-49177 | China | MK268235 | NA |
| *Pusillomyces manuripioides* | JO674 | Brazil | MK434210 | MK434211 |
| *Pu. manuripioides* | JO1121 | Brazil | MK434212 | MK434213 |

Note: "NA" = Not available in GenBank database. Specimens obtained from this study are in bold.

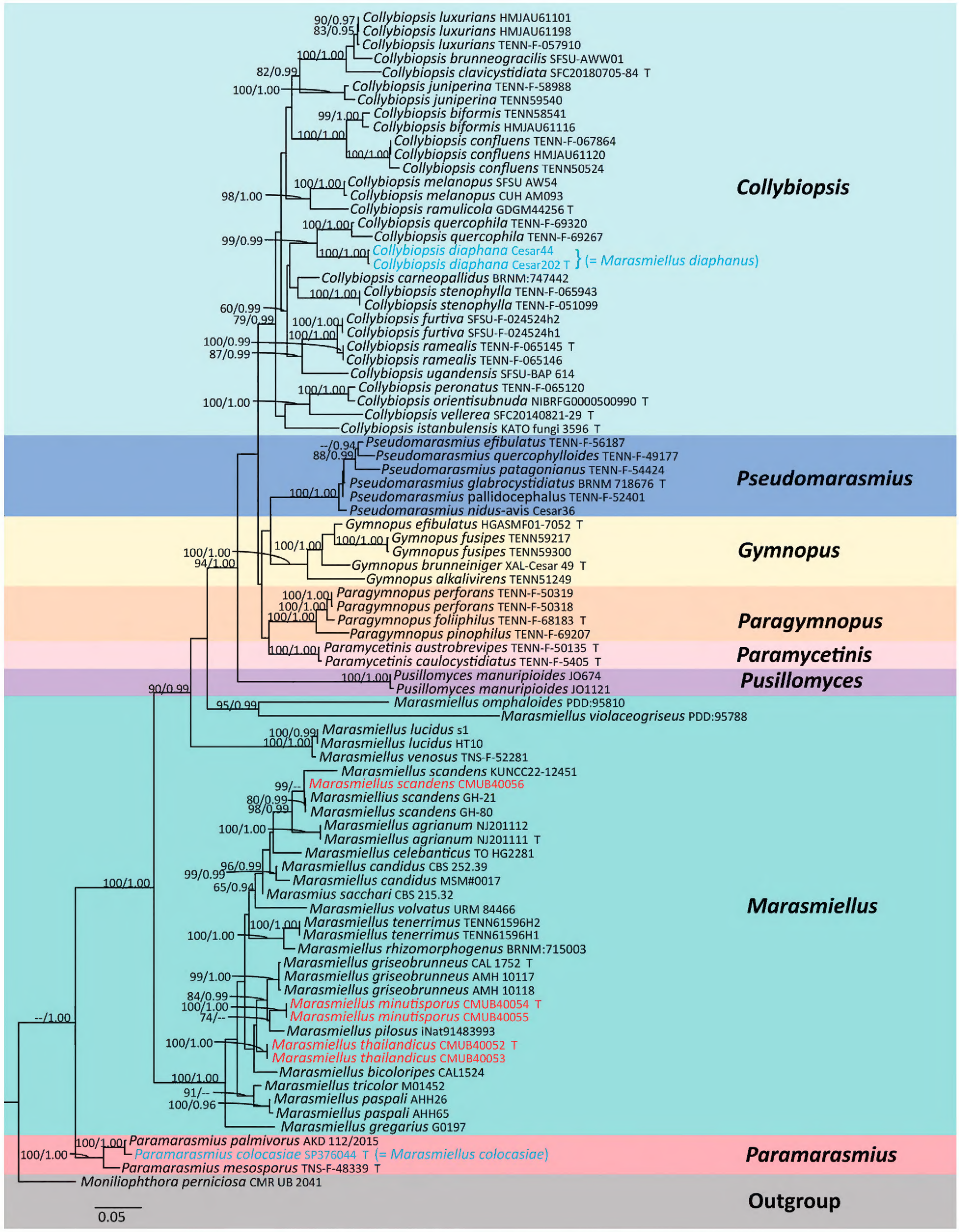


**Figure 1.** A combined phylogenetic tree was generated from maximum likelihood analysis (RAxML) based on a combined nrITS and nrLSU dataset. Bootstrap values (BS) ≥ 60% from ML analysis (left) and Bayesian posterior probabilities (right) (PP) ≥ 0.90 are shown on the branches. Newly sequenced collections are indicated in red, new combinations are in blue, and the type specimens are denoted by 'T'.

Two specimens in this study, CMUB40054, and CMUB40055, were clustered in a well-supported lineage (1.00 PP/100% BS), introduced as *M. minutisporus* related to *M. pilosus* (Dennis) Singer (iNat91483993), and sister to *M. griseobrunneus* Sharafudheen & Manim (AMH 10117, AMH 10118, and CAL1752) with a support value of 0.99 PP and 84% BS). The second species of this study (CMUB40052 and CMUB40053) formed a separate lineage within the genus *Marasmiellus* with higher support values (1.00 PP/100% BS) and formed a clade with *M. bicoloripes* K.P.D. Latha, K.N.A. Raj & Manim (CAL1524) and *M. minutisporus* cluster, and we introduced it as *M. thailandicus*. Additionally, one collection (CMUB40056) was clustered with *M. scandens* strain (GH80 and GH21) with strong statistical support (0.99 PP/100% BS). Noteworthily, *M. scandens* (KUNCC22-12451) differs from *M. scandens* (GH21) and (GH80) by 29 base pair differences out of 577, but our strain (CMUB40056) only has two base pair differences out of 570 bases (Fig. 1). Additionally, the phylogenetic tree showed that *M. diaphanus* César, Bandala & Montoya (Cesar 202 Type, and Cesar 44) belonged to *Collybiopsis* and formed a sister taxon to *C. quercophila* (Pouzar) R.H. Petersen (TENN-F-69320 and TENN-F-69267) with high statistical support (1.00 PP/99% BS; Fig. 1). *Marasmiellus colocasiae* Capelari & Antonín (SP376044, Type) assigned to the *Paramarasmius* and formed a sister taxon to *P. palmivorus* (Sharples) Antonín & Kolařík (AKD 112/2015) and clustered with *P. mesosporus* (Singer) Antonín, K. Hosaka & Kolařík (TNS-F-48339, Type) with strong support value (1.00 PP/98% ML; Fig. 1) in *Paramarasmius* Antonín & Kolařík branch. Therefore, based on phylogenetic analyses, *M. diaphanus* is proposed as *Collybiopsis diaphana* comb. nov., while *M. colocasiae* is proposed as *Paramarasmius colocasiae* comb. nov.

## Taxonomy

***Marasmiellus thailandicus* W. Lu, N. Suwannar. & J. Kumla, sp. nov.**

MycoBank: 854272

Figs 2A, B, 3

**Type.** Thailand • Chiang Mai Province, Chiang Mai University; 18°48'5"N, 98°57'23"E; elevation 337 m; on bark of *Lagerstroemia macrocarpa* Wall. ex Kurz, 5 August 2023, N. Suwannarach & J. Kumla (CMUB40052). GenBank accession numbers PP889929 (nrITS) and PP890009 (nrLSU).

**Etymology.** "*thailandicus*" refers to the country Thailand, where the type species was collected.

**Diagnosis.** Differs from *M. candidus* by the presence of a reddish gray to dull red, dry, radially wrinkled surface, grooved pileus with distant lamellae, and obovate or ellipsoid spores.

**Macrostructures.** ***Basidiomata*** small-sized, marasmioid. ***Pileus*** 6–20 mm diam., hemispherical first, expanding to plano-convex with slightly concave, radially sulcate with age, with involute then deflexed or straight margin, not distinctly hygrophanous, translucently striate up to center, reddish gray (10B2) to dull red (10B3) all over with grayish red (7B3) center, grayish red (7B3) margin, surface smooth, dry, and dull. ***Lamellae*** distant, broadly adnate to subdecurrent, sometimes anastomosing, white to cream-colored, with a reddish white (7A2) edge, particularly in young specimens, l = 2–3, L = 11–14. ***Stipe*** 4–8 × 1–2 mm, cylindrical, curved, base often slightly swollen, inconspicuous fibrils or scurfy, creamy-white

**Figure 2.** Habitat of *Marasmiellus* species in the present study **A**, **B** *Marasmiellus thailandicus* (CMUB40052, holotype) **C** *Marasmiellus minutisporus* (CMUB40054, holotype) **D** *Marasmiellus scandens* (CMUB40056, new record). Scale bars: 10 mm (**A–D**).

at apex, slightly reddish white (7A2) at the base, dry, pruinose all over, ***Context*** thin, fistulose or solid, concolorous with surface. ***Smell and taste*** indistinct.

**Microstructures.** ***Basidiospores*** (−12)13−16(−17) × 4−5(−6) µm (average = 15 × 5 µm), Q = (2.1)2.5−3.5(−3.75), Qm = 3.05 ± 0.38, sub-cylindrical to elongate with apiculus, inamyloid, thin-walled. ***Basidia*** 20−45 × 7−11 µm, 4-spored, clavate, sterigmata up to 5 µm. ***Cheilocystidia*** 50−53 × 8−13 µm, clavate. ***Pleurocystidia*** absent. ***Trama hyphae*** cylindrical, thin-walled, hyaline, inamyloid. ***Pileipellis***, a cutis with transitions to a trichoderm, made up of cylindrical; pigment brown, intracellular and minutely incrusting, hyphal 2−4 µm, negative in Melzer's reagent. ***Stipitipellis***, a cutis of parallel, somewhat skewed, cylindrical, or clavate-shaped, smooth hyphae, thin-walled, up to 7.5 um wide. ***Caulocystidia*** absent. ***Clamp connection*** present.

**Ecology and distribution.** Caespitose, in small groups growing on the bark of *Lagerstroemia macrocarpa*. Known only from the type locality in northern Thailand.

**Additional material examined.** THAILAND, • Chiang Mai Province, Chiang Mai University; 18°48'5"N, 98°57'23"E; elevation 337 m; on bark of *Lagerstroemia macrocarpa*, 24 August 2023, N. Suwannarach & J. Kumla (CMUB40053). GenBank accession numbers PP889930 (nrITS) and PP889930 (nrLSU).

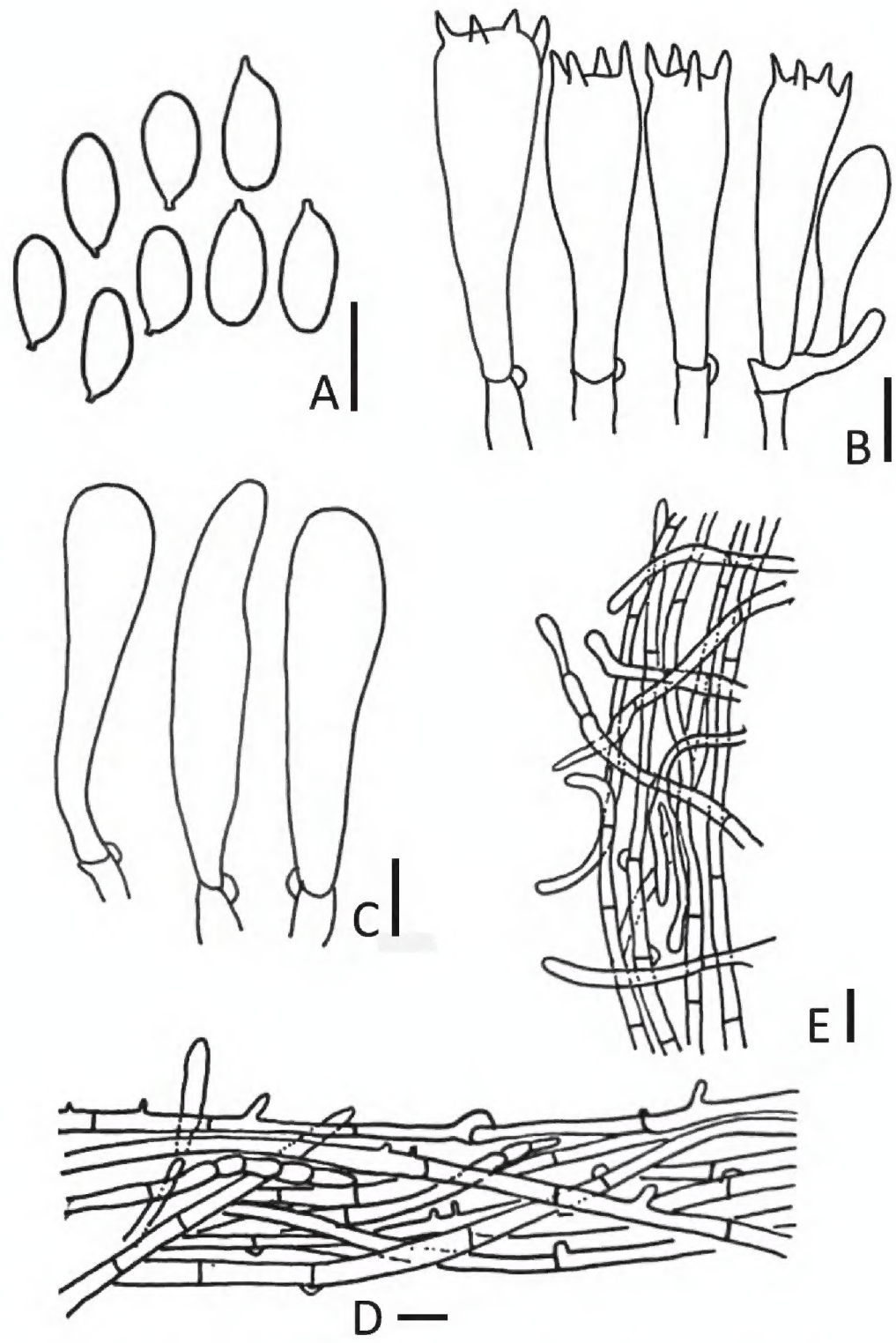


**Figure 3.** *Marasmiellus thailandicus* (CMUB40052, **holotype**) **A** basidiospores **B** basidia **C** cheilocystidia **D** terminal elements of pileipellis **E** hyphae of stipe. Scale bars: 10 µm (**A–E**).

***Marasmiellus minutisporus* W. Lu, P. Nutaratat & J. Kumla, sp. nov.**

MycoBank: 854273

Figs 2C, 4

**Type.** THAILAND • Phatthalung Province, Khuan Khanun, Sago Palm (*Metroxylon sagu*) Forest, 7°44'02"N, 99°59'47"E; elevation 23 m; on decaying leaf and branches of deciduous tree; 6 September 2023; P. Nutaratat, P., Suwannarach & J. Kumla, (CMUB40054). GenBank accession numbers PP889930 (nrITS) and PP890011 (nrLSU).

**Etymology.** "*minutisporus*" refers to the small basidiospores of this species.

**Diagnosis.** Differs from *M. virgatocutis* by the grayish-brown, convex, wrinkled pileus, longer pileus terminal, smaller elongated spores, and caulocystidia.

**Macrostructures.** ***Basidiomata*** small-sized, marasmioid. ***Pileus*** 5–11 mm diam., thin, then expanding to applanate, with slightly inflexed, pulvinate when young, then deflexed, finally reflexed, and undulating margin, convex when age with depressed to umbilicate at disc., grayish brown (7D3), often with grey, brown, or dark gray (1F1) at the center, gray at the margin; often radially wrinkled, surface dry, slightly pruinose to tomentose under the lens. ***Lamellae*** distant, often more or less reduced, white to sordid beige with a concolorous overall, pruinose edge, I = 1–3, L = 13–16.

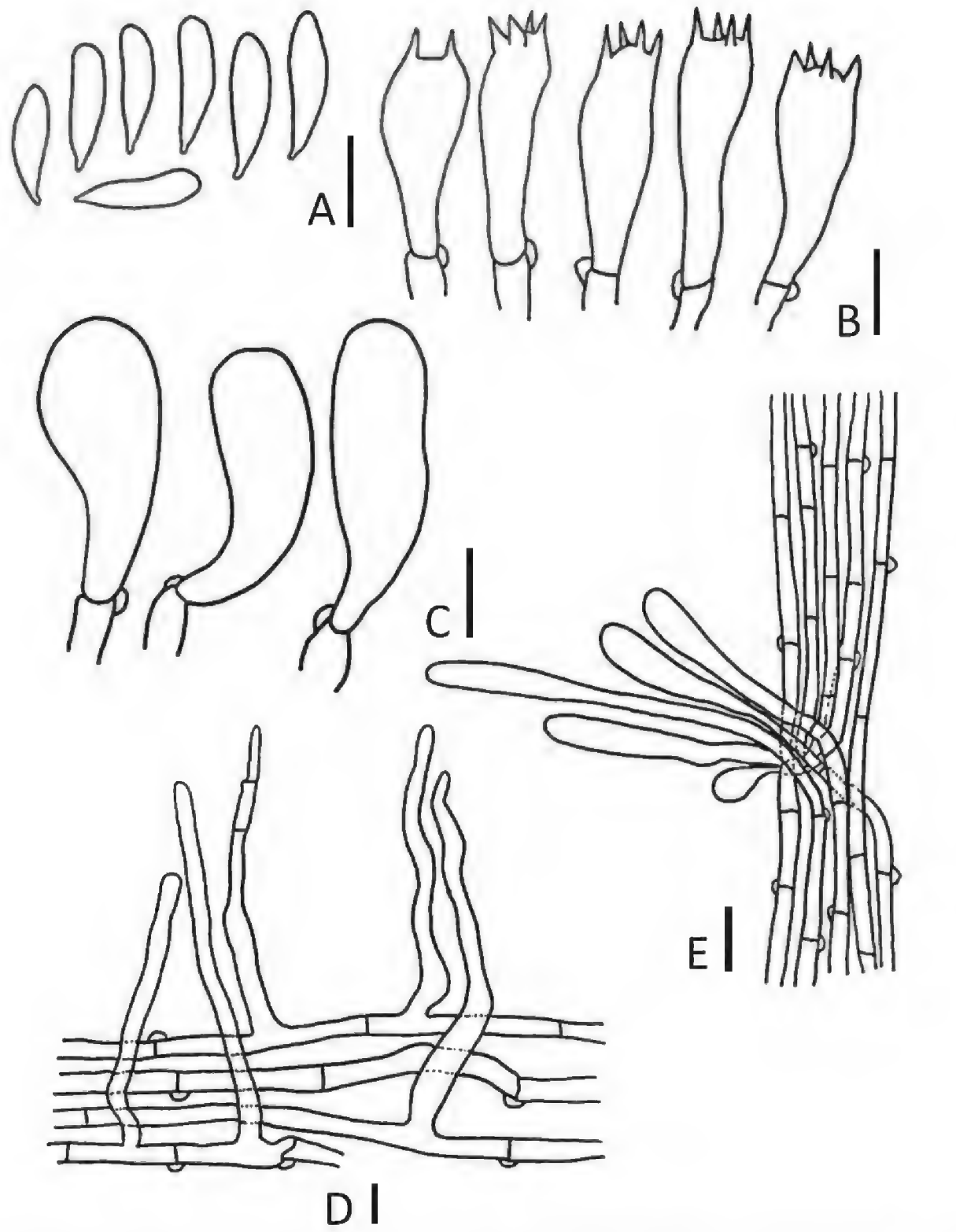


**Figure 4.** *Marasmiellus minutisporus* (CMUB40054, **holotype**) **A** basidiospores **B** basidia **C** cheilocystidia **D** elements of pileipellis **E** hyphae elements of stipe and caulocystidia. Scale bars: 5 µm (**A**); 10 µm (**B–E**).

***Stipe*** 4–9 × 1 mm, cylindrical, often subbulbous at the base, off-white at the apex, fourth to fifth downward, and black or gray at the stipe base, entirely white pruinose, with basal tomentum. ***Context*** thin, soft, white, fistulose. ***Smell and taste*** none.

**Microstructures.** ***Basidiospores*** (11)12–15(–16) × (3)4–5 µm (average = 14 × 4 µm), Q = (2.6)2.8–4(4.67), Qm = 3.5 ± 0.56, hyaline, inamyloid, cylindrical to fusiform, thin-walled. ***Basidia*** 25–28 × 7–9 µm, 4-spored, sterigmata up to 5 µm long, clavate. ***Lamella edge*** sterile. ***Cheilocystidia*** 30–33 × 12–15 µm, somewhat clavate to subglobose, ***Pleurocystidia*** absent. ***Pileipellis*** a cutis made up of 4.0–10 µm wide, inamyloid, inflated or cylindrical hyphae, with scattered suberect to erect, thin-walled, smooth, sometimes terminal elements up to 61–99 × 3.0–10 µm, gradually tapering to an acute or rounded apex. ***Stipitipellis*** a cutis composed of cylindrical, inamyloid, parallel, slightly, not incrusted, smooth, thick-walled. ***Caulocystidia*** 25–50 × 4–5 µm, adpressed to erect, cylindrical, clavate, smooth, thin-walled. ***Clamp connection*** present.

**Ecology and distribution.** Solitary to caespitose, in small groups growing on decaying leaves and twigs of deciduous trees. Known only from the type locality in southern Thailand.

**Additional material examined.** THAILAND • Phatthalung Province, Khuan Khanun, Sago Palm (*Metroxylon sagu*) Forest, 7°44'02"N, 99°59'46"E; elevation 23 m; on decaying leaf and twigs of deciduous tree; 7 September 2023; P. Nutaratat, N. Suwannarach & J. Kumla, (CMUB40055). GenBank accession numbers PP889932 (nrITS) and PP890012 (nrLSU).

***Marasmiellus scandens* (Massee) Dennis & D.A. Reid, *Kew Bull.* [11](2): 289 (1957)**

MycoBank: 300136

Figs 2D, 5

**Macrostructures.** ***Basidiomata*** small-sized, marasmioid. ***Pileus*** 5–10 mm diam., orbicular when young and then convex at age, streaked from disc to margin, margin entire, wavy to irregular, decurved or greatly reflexed, surface dry, smooth, white pruinose, white to grayish orange (5B4–5), grayish orange (5B4) at the margin. ***Lamellae*** adnate, subdistant, with 2–3 series of lamellulae, 14–16 major lamellae, unequal, narrow, pale white at face and edge. Smell and taste none. ***Stipe*** 4–6 × 1–2 mm, often curved, lateral or central, disc at the base, dry, surface smooth, whitish to pale orange (5A3); Context thick, fistulose, orange white (5A2–3).

**Microstructures.** ***Basidiospores*** 7–9(–10) × (3)3.5–4.5(–6) µm (average = 8 × 4.5 µm), Q = 1.4–1.8(–2), Qm = 1.74 ± 0.11, broadly ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia 10–12.5 × 3–4.5 µm, clavate, 4-spored, sterigmata up to 1.5 µm. ***Cheilocystidia*** abundant, 15–17(–22) × 8–9(–11) µm, broom-cell type with finger-like excrescences in the upper half, hyaline, thin-walled. ***Pleurocystidia*** absent. ***Pileipellis*** with poorly ***Ramealis***-structure, ***trama*** hyphae 4–9 µm, negative in Melzer's reagent. ***Stipitipellis*** hyphae up to 5 µm wide, smooth, thin-walled, ***trama*** not observed, negative in Melzer's reagent. ***Clamp connections*** present.

**Ecology and distribution.** Caespitose, in small groups on decaying leaf of *Metroxylon sagu* in southern Thailand (This study), on *Aquilaria sinensis* (agarwood) trees in China (Zhang et al. 2023), and on the stem of mangosteen in Malaysia (Turner 1971), on cocoa in Australia, Ghana, Caribbean, Papua New Guinea, and Solomon Islands (Amoako-Attah et al. 2020; Ali et al. 2021), on coffee in Fiji, Guinea, and Sierra Leone (Lu et al. 2022).

**Material examined.** THAILAND • Phatthalung Province, Khuan Khanun, Sago Palm (*Metroxylon sagu*) Forest, 7°44'02"N, 99°59'47"E; elevation 24 m; on decaying leaf of *Metroxylon sagu*; 3 September 2023; P. Nutaratat, N. Suwannarach & J. Kumla, (CMUB40056). GenBank accession numbers PP889933 (nrITS) and PP890013 (nrLSU).

## New combinations

***Collybiopsis diaphana* (César, Bandala & Montoya) W. Lu, N. Suwannar. & J. Kumla, comb. nov.**

MycoBank: 854271

≡ *Marasmiellus diaphanus* César, Bandala & Montoya, in César, Montoya, Bandala & Ramos, *Mycol. Progr.* 19(10): 1022 (2020)

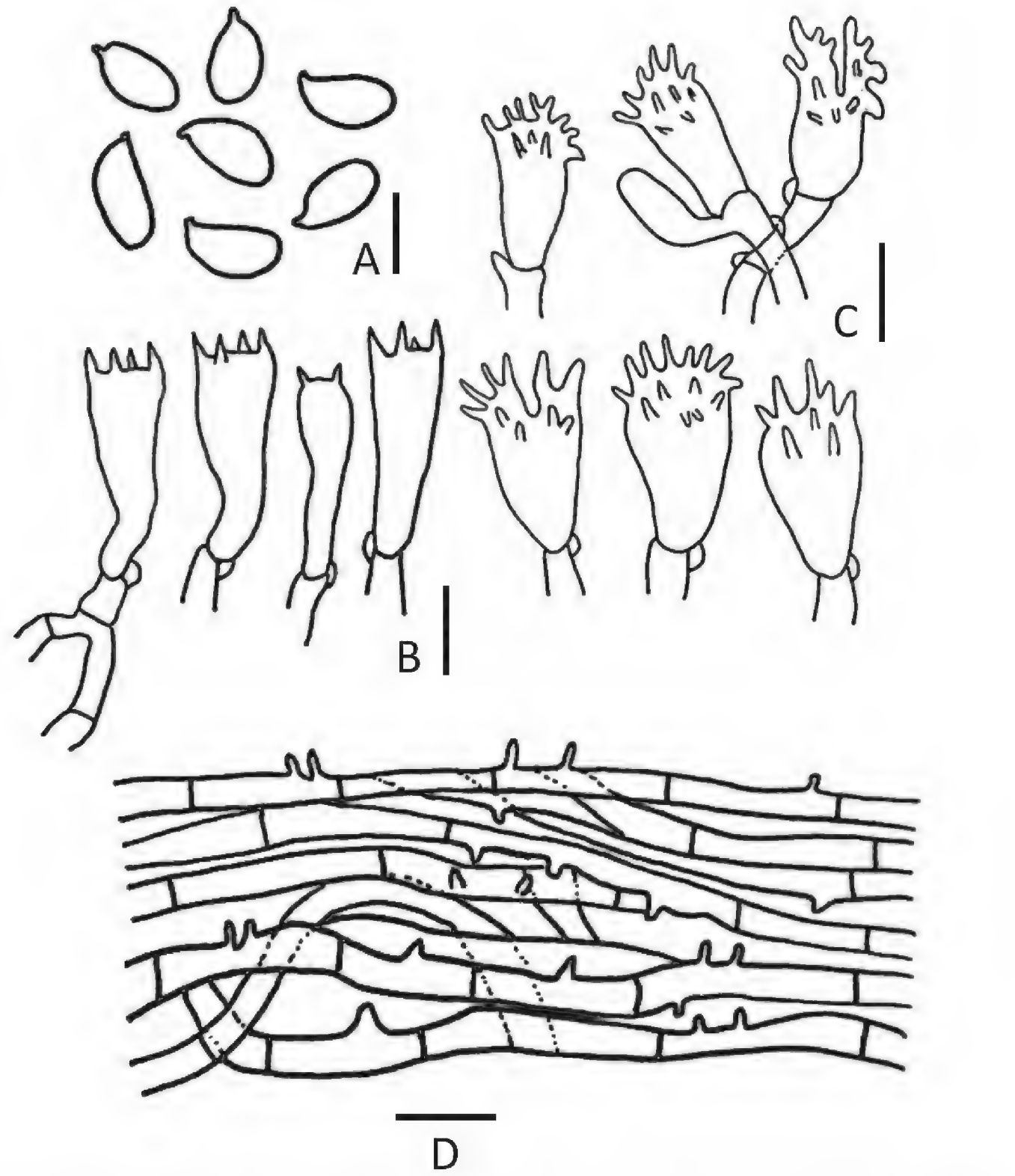


**Figure 5.** *Marasmiellus scandens* (CMUB40056, new record) **A** basidiospores **B** basidia **C** cheilocystidia **D** terminal elements of pileipellis. Scale bars: 5 μm (**A–C**); 10 μm (**D**).

***Paramarasmius colocasiae*** **(Capelari & Antonín) W. Lu, N. Suwannar. & J. Kumla, comb. nov.**

MycoBank: 854270

≡ *Marasmiellus colocasiae* Capelari & Antonín, *Cryptog. Mycol.* 31(2): 138 (2010)

## Discussion

A combination of morphological characteristics and molecular phylogeny inferred from sequence data of the nrITS and nrLSU region revealed two new species of *Marasmiellus* (*M. thailandicus* and *M. minutisporus*) and one known species (*M. scandens*) in this study. According to the phylogeny results, *Marasmiellus* is well-clustered in a strongly supported clade (1.00 PP/100% BS) (Fig. 1), which is consistent with the results of previous phylogenetic studies (Sesli et al. 2018; Sharafudheen and Manimohan 2019; César et al. 2020). Furthermore, the phylogenetic tree indicated that *M. diaphanus* and *M. colocasiae* belonged to *Collybiopsis* and *Paramarasmius*, respectively. Therefore, these two new combinations were introduced as *C. diaphana* and *P. colocasiae*.

Morphologically, *M. thailandicus* is closely related to *M. subnigricans* (Murrill) Singer, *M. candidus*, and *M. bicoloripes*. *Marasmiellus subnigricans* (11–45 mm diam.) and *M. candidus* (3–22 mm diam) contain dingy cream and purely white to sordid white (Antonín and Noordeloos 2010; Retnowati 2018). However, *M. subnigricans* differs from *M. thailandicus* by having smaller basidia (24–32 × 8–8.8 µm), hygrophanous, subtranslucent to strongly translucent pileus, and longer stipe (13–50 × 1–3 mm), and larger basidiospores (13.6–17.6 × 4–5.6 µm). *Marasmiellus candidus* has white grooved, large pileus with a tendency to develop pinkish tinges at age, brown and swollen at the base, long, slender neck cheilocystidia, and caulocystidia, as well as large pileus (Antonín and Noordeloos 2010). *Marasmiellus bicoloripes* is distinguished from *M. thailandicus* by having smaller basidiospores (4–8 × 3–4 µm) and pileipellis without setae. Phylogenetically, *M. thailandicus* formed a monophyletic clade and separated other *Marasmiellus* species with strong statistical support.

Based on morphological characteristics, *M. minutisporus* is closely related to *M. virgatocutis* Robich, Esteve-Rav. & G. Moreno and *M. griseobrunneus*. However, *M. virgatocutis* is distinguished by the radially fibrillose-virgate pileus surface and the variable shape of cheilocystidia, which range from clavate to lageniform to molariform. While *M. griseobrunneus* has a surface of dark brown, the largest pileus (8–38 mm diam.), and observed pleurocystidia compared with *M. minutisporus* (Sharafudheen and Manimohan 2019). Phylogenetically, *M. minutisporus* is closely related to *M. pilosus*. However, *M. minutisporus* differs from *M. pilosus* in that it is grayish-brown, convex, wrinkled pileus with a fimbriate margin and the absence of pleurocystidia (Singer 1973).

*Marasmiellus scandens* was previously reported worldwide (in Asia, Africa, Oceania, and North America) as a pathogen and endophytic form in cocoa and coffee (Amoako-Attah et al. 2020; Ali et al. 2021; Lu et al. 2022; Zhang et al. 2023). In this study, the Thai specimen is similar to the descriptions of Dennis and Reid (1957) from *M. scandens*, originally described as *Marasmius scandens* by Massee (1910). However, Thai specimens mostly differed from Chinese specimens (HKAS-124582) (Zhang et al. 2023) in the shape of cheilocystidia with a broom-cell type. This may be influenced by the phenotypic variability across a wide geographic range.

Prior to the present study, eight species of *Marasmiellus* have been reported based on morphological characteristics in Thailand viz. *M. albofuscus*, *M. alliiodorus*, *M. amygdalosporus*, *M. candidus*, *M. chamaecyparidis*, *M. collybioides*, *M. corticum*, and *M. paspali* (Chandrasrikul et al. 2011; Seephueak et al. 2018). Most of them are widely found in Asia (China, Indonesia, and Japan), North America (Hawaii and Florida), South America (Argentina, Brazil, and Chile), the Caribbean (Cuba and the Lesser Antilles), and Oceania (Hongo 1975; Jackson and Firman 1982; Kohler et al. 1997). Some are only known in South America (*M. alliiodorus*) and West Africa (*M. paspali*) (Spegazzini 1889; Singer 1962; Pegler 1977; Buadu et al. 2002; Deng et al. 2011; Zhu et al. 2024). Historically, Thai macrofungi have been classified and described based on morphological characteristics. Of them, some are associated with the species previously known only in America, Europe, and other continents (Suwannarach et al. 2022a, b). Therefore, these eight species require further confirmation through newly collected specimens

identified based on morphology and phylogeny. Additionally, this finding has increased the number of *Marasmiellus* species found in Thailand to 11. Finally, this finding is important in stimulating future studies of *Marasmiellus* in Thailand and contributes to distribution, diversity, phylogeny, and classification in Asia and worldwide.

## Acknowledgments

The authors thank Shaun Pennycook for the nomenclatural advice and Russell Kirk Hollis for his help with the English correction.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Funding

This work was supported by Chiang Mai University and National Higher Education, Science Research and Innovation Policy Council, Thaksin University Research Grant Fiscal Year 2023, Thailand. Nakarin Suwannarach and Samantha C. Karunarathna thank CMU Visiting Researcher 2024, Chiang Mai University (Grant number CMUVP038/2567), Thailand. Samantha C. Karunarathna and Saowaluck Tibpromma thank the National Natural Science Foundation of China (No. 32260004), Yunnan Revitalization Talents Support Plan (High-End Foreign Experts and Young Talents Programs), and the Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River. The authors extend their appreciation to the Deputyship for Research and Innovation, "Ministry of Education" in Saudi Arabia for funding this research (IFKSUOR3-299-19).

### Author contributions

Conceptualization: NS, SCK. Data curation: WL, JK, PN. Investigation: WL, NS, JK, PN, ST, SCK. Project administration: NS, SCK. Software: WL, JK. Supervision: NS, SCK. Writing-review and editing: WL, NS, JK, PN, ST, AME, SCK.

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### Data availability

All of the data that support the findings of this study are available in the main text

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